**RESEARCH ARTICLE**

# Predation risk by largemouth bass modulates feeding functional responses of native and non-native crayfish

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## Abstract

Context-dependency is prevalent in nature, challenging our understanding and prediction of the potential ecological impacts of non-native species (NNS). The presence of a top predator, for example, can modify the foraging behaviour of an intermediate consumer, by means of non-consumptive effects. This raises the question of whether the fear of predation might modulate consumption rates of NNS, thus shaping the magnitude of ecological impacts. Here, we quantified the functional feeding responses of three non-native crayfish species – red swamp crayfish *Procambarus clarkii*, rusty crayfish *Faxonius rusticus* and virile crayfish *Faxonius virilis* – compared to the native analogue signal crayfish *Pacifastacus leniusculus*, considering the predation risk imposed by a top fish predator, the globally invasive largemouth bass *Micropterus salmoides*. We applied the comparative functional response (FR) approach using snails as prey and exposing crayfish to water containing predator and dietary chemical cues or not. All crayfish species presented a destabilising Type II FR, regardless of the presence of chemical cues. Predation risk resulted in significantly longer handling times or lower attack rates in non-native crayfish; however, no significant differences were observed in signal crayfish. We estimated *per capita* impacts for each species using the functional response ratio (FRR; attack rate divided by handling time). The FRR metric was lower for all crayfish species when exposed to predation risk. Rusty crayfish demonstrated the highest FRR in the absence of chemical cues, followed by signal crayfish, virile crayfish and red swamp crayfish. By contrast, the FRR of signal crayfish was nearly twice that of rusty crayfish and virile crayfish and ten times greater than red swamp crayfish when chemical cues were present. The latter result agrees with the well-recognised ecological impacts of signal crayfish throughout its globally-introduced range. This study demonstrates the importance of considering the non-consumptive effects of predators when quantifying the ecological impacts of intermediate non-native consumers on prey. The direction and magnitude of the modulating effects of predators have clear implications for our understanding of NNS impacts and the prioritisation of management actions.

## Introduction

Non-native species (NNS) are a primary driver of environmental change, with negative impacts on individuals to entire ecosystems and severely disrupting important services provided by nature (Ricciardi et al. 2013). Economic burdens are also concerning, with estimated costs to prevent and control NNS impacts exceeding a hundred million dollars per year globally (Pyšek et al. 2020; Diagne et al. 2021), possibly increasing in the future (Ahmed et al. 2022). Management and policy strategies rely on identifying the most impactful species to help target prevention efforts and allocate limited resources to control or eradicate burgeoning populations. Still, this task is challenging due to variations in NNS impacts, based on ecosystem, geographical location, time since establishment and individual values (Závorka et al. 2018; Santos et al. 2019). Considering the increasing rate of invasions, comparative studies of the context-dependency of NNS impacts will help prioritise which species should be managed in the future (Lockwood et al. 2007; Dick et al. 2017a; Seebens et al. 2017).

Quantifying *per capita* effects of NNS remains central to most frameworks evaluating their ecological impacts (Parker et al. 1999; Kumschick et al. 2015; Griffen et al. 2020). Given the challenges of estimating *per capita* effects, focus has shifted to the use of experiments to quantify resource consumption rates as a proxy (Dick et al. 2017b). Non-native consumers often consume resources more efficiently than their native counterparts (Funk and Vitousek 2007; Salo et al. 2007; Paolucci et al. 2013), making comparative rates of consumption between native and NNS a useful currency to anticipate negative impacts from species introductions (Dick et al. 2014).

The fundamental ecological concept of functional responses (FR) – resource use as a function of availability – provides a measurable estimate of the *per capita* effect of a consumer on a given resource (Solomon 1949; Holling 1959; Dick et al. 2014). Type I FR describes a linear relationship between consumption and resource availability, typical of filter-feeding species (Jeschke et al. 2004). Type II FRs are destabilising due to high consumption rates at low resource densities, while Type III FRs promote stabilising effects due to low consumption rates when resources are scarce (Oaten and Murdoch 1975). The utility of FRs lies in comparing the maximum consumption rate between NNS and native trophic analogues in the same environmental context (Dick et al. 2014, 2017a), making this approach increasingly applied to quantify and predict ecological impacts of NNS (Faria et al. 2023).

The comparative FR approach enables the evaluation of *per capita* effects in different contexts, allowing more realistic and practical impact assessments (Dick et al. 2017a; Dickey et al. 2020). Despite this, investigations involving trophic levels beyond the focal consumer-resource interaction remain limited (e.g. Barrios-O'Neill et al. (2014); Paterson et al. (2015)). Foraging behaviour and consumption rates of

consumers are sensitive to the presence of higher-order predators, which invoke trade-offs in resource acquisition versus mortality risk by predation (Lima and Dill 1990; Brown and Kotler 2004). Fear of predation can shape entire ecosystems through trait-mediated indirect effects (TMIEs) on prey traits, such as behaviour and physiology (Werner and Peacor 2003; Peckarsky et al. 2008; Laundré et al. 2010). In some circumstances, the non-consumptive effects of predators are thought to be as strong as direct consumption for population dynamics, leading to greater system stability (Brown et al. 1999) or even causing trophic cascades (Schmitz et al. 2004; Preisser et al. 2005; Peckarsky et al. 2008).

Trait-mediated indirect effects are particularly prominent in freshwater ecosystems, likely due to the effective transmission of visual and chemical cues indicating predator presence (Preisser et al. 2005). For example, the presence of largemouth bass (*Micropterus salmoides*) altered the foraging behaviour and habitat use of bluegill sunfish (*Lepomis macrochirus*) prey leading to cascading changes in zooplankton communities (Turner and Mittelbach 1990). In another example, rusty crayfish (*Faxonius rusticus*) displayed greater consumption of macrophytes when exposed to chemical cues from largemouth bass, suggesting a robust effect of predation risk on crayfish foraging behaviour (Wood et al. 2018).

Despite the strong effects of non-consumptive effects in shaping communities, they are relatively underexplored compared to consumptive effects in the context of quantifying NNS impacts. Applying the comparative FR approach, we aim to test whether the non-consumptive effects of a top predator, the non-native largemouth bass, mediate the consumptive impacts of three non-native crayfish species (*Procambarus clarkii*, *Faxonius virilis* and *F. rusticus*) and a native analogue (*Pacifastacus leniusculus*) preying on snails. We hypothesise that non-consumptive effects of a top predator will reduce consumption rates of all crayfish species, but to a lesser extent for non-native crayfish with a shorter evolutionary history with the predator. The differential response to predation risk imposed by the largemouth bass may explain the expected higher *per capita* effects of non-native consumers compared to native analogue species.

## Methods

### Study system

Our study system is a three-level food chain composed by a non-native top predator, the largemouth bass, an intermediate consumer represented by non-native or native crayfish (Table 1) and native freshwater snails (Gastropoda, Planorbidae) as the basal resource. Crayfish are known to be highly sensitive to different chemical cues such as predator odour, dietary and alarm cues (Beattie and Moore 2018; Wood et al. 2018; Wood and Moore 2020a, b) and these cues show utility in assessing TMIEs (Paterson et al. 2013). Thus, we used a combination of predator and dietary chemical cues to provide the biological context of predation risk in our comparative FR approach.

**Table 1.** Crayfish species examined in this study, including scientific and common names, history of introduction in the Pacific Northwest region, sampled populations (coordinates) and carapace length (CL) and mass, presented as the mean (SD), of the individuals used in the experiments.

| Crayfish | Scientific name | Common name | Estimated time of introduction | Sampled population | CL (mm) | Mass (g) |
|---|---|---|---|---|---|---|
|  | *Pacifastacus leniusculus* | Signal crayfish | Native | Skykomish River, WA (47.8482, -121.8403) | 50.2 (4.3) | 36.9 (10.3) |
|  | *Procambarus clarkii* | Red swamp crayfish | 1970s | Pine Lake, WA (47.5907, -122.0389) | 53.6 (5.7) | 39.7 (13.0) |
|  | *Faxonius rusticus* | Rusty crayfish | 2005 | Magone Lake, OR (44.5486, -118.9119) | 41.1 (3.1) | 25.9 (5.3) |
|  | *Faxonius virilis* | Virile crayfish | 1980s | Rattlesnake Lake, WA (47.4308, -121.7715) | 46.0 (3.5) | 32.6 (7.6) |

The geographic context of the study is the Pacific Northwest region of the US, where all species were sourced (Table 1). The apex predator largemouth bass has a native distribution that extends from north-eastern US to northern Mexico (Brown et al. 2009), with a long history of intentional introduction for recreational fishing in many regions of the US and the world, including the study region dating back to the beginning of the 20th century (Stein 1970). The non-native crayfish used in this study have a varied history of introductions in the region (Table 1) and are amongst the most widespread and harmful invasive crayfish species in the world (Twardochleb et al. 2013). Signal crayfish is the most widely distributed native crayfish species in the region (Larson and Olden 2011) and also highly invasive outside its native range (Usio et al. 2007; Twardochleb et al. 2013; Vaeßen and Hollert 2015). All crayfish species used in this study are omnivorous and nocturnal, presenting maximum feeding or growth rates between 20 and 30 °C (Crandall and Buhay 2008; Westhoff and Rosenberger 2016; Rodríguez Valido et al. 2021; Ruokonen and Karjalainen 2022).

## Animal collection and maintenance

Largemouth bass were collected using electrofishing from Lake Washington, WA (47.6469, -122.2991) in October 2022. A total of 33 fish were captured and transported to the lab facility at the University of Washington, where they were maintained in a circular tank of approximately 800 l without shelter (hereafter stimulus tank), aerated and continuously filled with water from Lake Washington, in an open circulation system (mean total length = 194 mm, SD = 53). Fish were acclimatised to the stimulus tank for two weeks before the beginning of the trials.

A total of 433 crayfish were sampled using baited traps deployed overnight from lakes in Washington and Oregon States in October 2022 (Table 1). Crayfish were kept in tanks of 256 l separated by species, with a maximum stock density of 30 individuals per tank. Stock tanks were continuously filled with water from Lake Washington, in an open circulation system and contained abundant structure for shelter. Crayfish were fed daily with commercial algae pellets until satiation and were acclimatised for at least two weeks before being used in the experiment. Snails used as prey were obtained from various commercial pet retailers (shell length mean = 10.3 mm, SD = 2.4). Snails were kept in a separate tank, in the same conditions as crayfish.

## Functional response experiments

Native and NNS of crayfish were tested for differences in their predatory rate of snail prey supplied in seven different initial densities (2, 4, 8, 12, 16, 24 and 40 snails) under the presence or absence of waterborne predator and dietary chemical cues (hereafter, predator treatment and control, respectively). Experiments were conducted in a fully-randomised design with respect to crayfish species and initial prey densities assigned to predator treatment and control. Experimental arenas were round opaque tanks (44.5 cm diameter, 42.5 cm height) filled with 10 l of water and no substrate or shelter were provided (Fig. 1A). At the predator treatment, water was supplied from the stimulus tank containing water from Lake Washington and bass (Fig. 1B), whereas under the control, just water from Lake Washington was supplied (as in the stock tanks) (Fig. 1C). Lake Washington water is piped directly from 10 m depth where largemouth bass and other fish species are at low abundance. Water was supplied continuously by dripping through small hoses (5 mm diameter) to ensure that chemical cues were present throughout the experiment (Fig. 1D). Water temperature in experimental arenas and stock tanks were similar, all demonstrating natural diel ranges of 12.5°–18.5 °C.

Fish were starved for a week and then fed every other day a diet of crayfish before and during the experiments. Small individuals of all crayfish species were supplied simultaneously until satiation to enhance the response of crayfish to conspecific dietary cues released by the fish (Beattie and Moore 2018; Wood et al. 2018). Crayfish were starved in a separate tank for 48 h before use in experiments to standardise hunger levels. After the starvation period, an individual crayfish was allocated to each
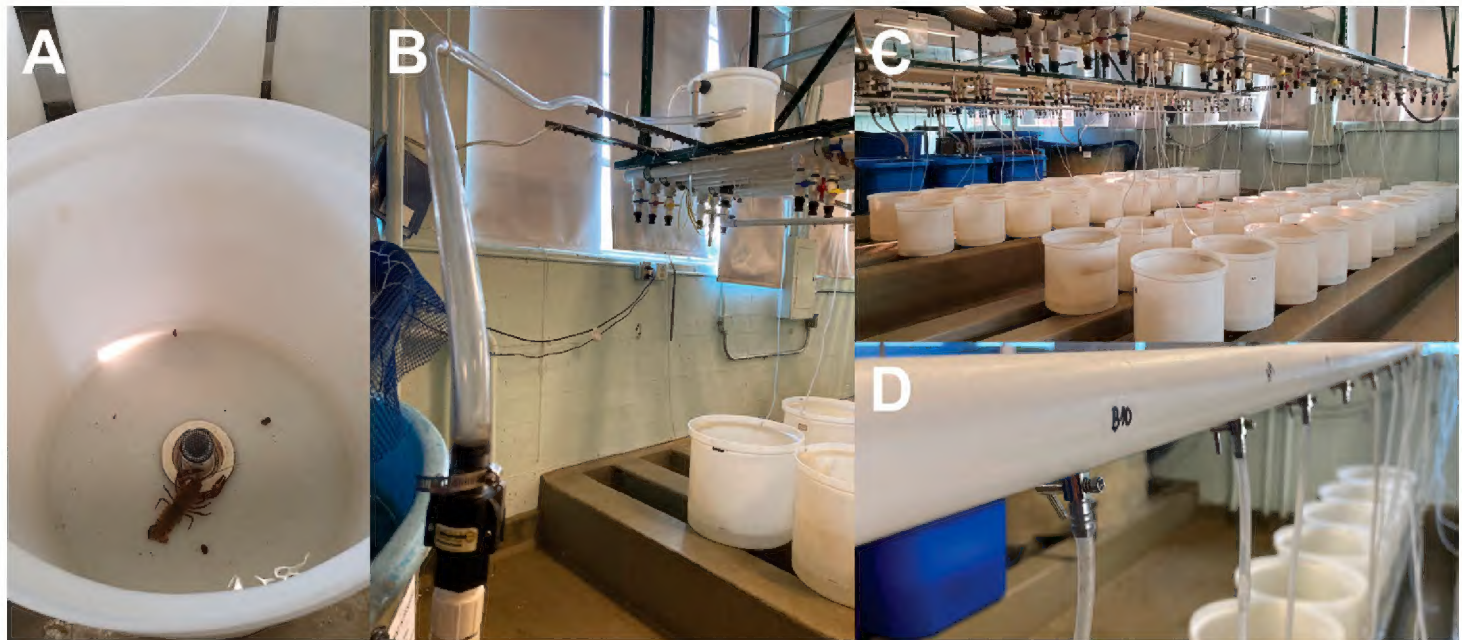
**Figure 1.** Experimental setup used in the functional response trials **A** experimental arena with a signal crayfish and snail prey during a trial **B** water from the tank containing largemouth bass (left) was pumped to a head tank (upper right) and **C** distributed to the experimental arenas in the predator treatment (upper-left row) or water was supplied directly from Lake Washington to the control arenas (lower-right row). Blue tanks in the background were stock and starvation tanks where crayfish were kept before being used in trials **D** the water from both treatments was supplied to each experimental arena via individually controlled hoses.

experimental arena containing one of the seven initial densities of prey and allowed to forage for 24 h. The number of remaining prey was recorded at the end of the trials, along with the number of attacked, but uneaten prey. Crayfish sex, carapace length (CL) and mass were recorded, as well as the water temperature at the end of the trial.

There were seven replicates for each combination of crayfish species, initial density of prey and treatment. At least five replicates of each combination were performed in the absence of crayfish to account for any background mortality of prey. Prey survivorship in these replicates was 99.9%, thus all prey deaths during experiments were attributed to crayfish predation. Crayfish were not reused in the experimental trials and replicates where crayfish moulted during the trial or one week after were repeated.

## Data analysis

All statistical analyses were carried out in R version 4.1.2 (R Core Team 2021). Functional response analyses were conducted using the number of prey consumed as the response variable, under the frair package (Pritchard et al. 2017). For each crayfish species × treatment combination, FR type was determined by logistic regression of the proportion of prey consumed against initial prey density (Juliano 2001). If the proportion of prey consumed decreases with increasing prey density, it produces a significantly negative first-order term, indicating a Type II FR; if otherwise, a significantly positive first-order term is obtained then it indicates a Type III FR (Juliano 2001). When the results of the logistic regression were not conclusive, different FR

models were fitted directly and compared using Akaike's Information Criterion (AIC) (Pritchard et al. 2017).

Based on these analyses, all FRs were then modelled as Type II. Maximum Likelihood model fitting was used to fit data to the Rogers' random predator equation (Rogers 1972) that accounts for the depletion of prey along the experimental duration:

$$N_e = N_0(1 - \exp(a(N_e h - T)))$$

where $N_e$ is the number of prey consumed, $N_0$ is the initial density of prey, $a$ is the attack rate, $h$ is the handling time and $T$ is the time available for predation in days (i.e. experimental duration). As $N_e$ is obtained experimentally, the estimated FR parameters are attack rate and handling time, representing a measure of successful attacks and the time needed for a predator to handle and ingest a prey item, respectively. The Lambert W function is implemented to solve the fact that $N_e$ appears on both sides of the equation (Bolker 2008).

To compare FR parameters $a$ and $h$ between predator treatment and control, we used the indicator variables method (Juliano 2001; Pritchard et al. 2017), as:

$$0 = N_0 - N_0 \exp\{[a + D_a(j)]\{[h + Dh(j)](N_e) - T\}\} - N_e$$

where $j$ is an indicator variable that takes value 0 for control and 1 for predator treatment. The parameters $Da$ and $Dh$ estimate the differences between treatments in the value of the parameters $a$ and $h$, respectively. If $Da$ and $Dh$ are significantly different from zero, then the estimated FR parameters differ between treatment and control (Juliano 2001). The maximum feeding rate of each crayfish species × treatment combination was calculated as $1/(hT)$ indicating the maximum number of prey that one crayfish can consume in one day (T = 1 day). Additionally, the functional response ratio (FRR) was calculated, as a comparative metric of the ecological impact of NNS (Cuthbert et al. 2019), dividing the attack rate parameter by the handling time ($a/h$). High values of FRR are indicative of strong *per capita* impacts, while low values indicate less impactful predators (Cuthbert et al. 2019).

Potential differences in the trial's water temperature amongst species and initial densities of prey were evaluated through Kruskal-Wallis tests, as well as differences in crayfish weight and carapace length (CL) amongst species and initial densities of prey. Water temperature in trials did not vary amongst species (Kruskal–Wallis $X^2(3) = 7.366$, $p = 0.06$) nor in association with the initial densities of prey tested (Kruskal–Wallis $X^2(6) = 11.339$, $p = 0.08$). Crayfish mass and carapace length varied amongst species (Mass: Kruskal–Wallis $X^2(3) = 96.73$, $p < 0.001$; CL: Kruskal–Wallis $X^2(3) = 224.73$, $p < 0.001$). The effect of crayfish size and sex on the proportion of prey consumed was investigated with Spearman's correlation and Mann-Whitney tests, respectively. Crayfish size (Mass: r = 0.01, $p = 0.84$; CL: r = -0.08, $p = 0.12$) and sex (Mann-Whitney U = 14828, $p = 0.74$) had no relation to the proportion of prey consumed.

## Results

All crayfish species presented a destabilising Type II FR towards snail prey, regardless of the presence of chemical cues (Fig. 2). This was confirmed by the significantly negative first-order term of the logistic regression, except for red swamp crayfish under predator treatment and rusty crayfish under control, where the estimates were non-significant (Table 2). For these two specific cases, the FR type was determined by comparing the AIC of different model fittings. For red swamp crayfish, Type I had a lower AIC ($\Delta$AIC = 0.8), while for rusty crayfish, Type II presented a better fit ($\Delta$AIC = 1.1) compared to other models (generalised FR model, Type I and Type III).

Non-consumptive effects were observed for all non-native crayfish species, except for native signal crayfish (Fig. 2). Predation risk lowered the magnitude of the FR, which reflects reduced maximum consumption rates estimated in the predator treatment compared to the control (Table 2). These differences were driven by significantly longer handling time of snails for virile crayfish ($Dh$ = -0.03 $\pm$ 0.008, $p$ < 0.001) and rusty crayfish ($Dh$ = -0.02 $\pm$ 0.008, $p$ = 0.01) (Fig. 3A) and significantly lower attack rate displayed by red swamp crayfish ($Da$ = 0.25 $\pm$ 0.09, $p$ = 0.006) (Fig. 3B) in the presence of chemical cues. No significant differences in handling time or attack rates were evidenced for signal crayfish between treatment and control.

Native signal crayfish demonstrated a greater consumption rate when exposed to predation risk compared to non-native crayfish (Fig. 2). *Per capita* effects of signal crayfish on snails, according to the FRR, was nearly twice that of rusty crayfish and virile crayfish and ten times greater than red swamp crayfish (Fig. 4, Table 2). By contrast, rusty crayfish demonstrated the highest FRR in the control, followed by signal crayfish, virile crayfish and red swamp crayfish (Fig. 4, Table 2).

## Discussion

Predators can exert non-consumptive effects on prey that are comparable in magnitude to consumptive effects (Werner and Peacor 2003; Preisser et al. 2005). Despite that, non-consumptive effects remain largely under-studied in evaluations of ecological impacts of NNS (Sih et al. 2010). Here, we quantified rates of snail predation by multiple non-native and a native crayfish species in the presence or absence of chemical and dietary cues from a higher-order predator. We found that predation risk reduced maximum consumption rates of snails due to longer handling times or lower attack rates, but did not alter the shape of the FR curve. Reduced foraging activity is a common antipredator behavioural response of crayfish when exposed to predation risk (Gherardi et al. 2011b; Beattie and Moore 2018; Kenison et al. 2018). For example, red swamp crayfish significantly reduces the time spent feeding by adopting a lowered posture after being exposed to largemouth bass cues (Gherardi et al. 2011b).

Native signal crayfish was the only study species demonstrating little evidence for the effect of predation risk on the FR magnitude. This outcome is supported by a body
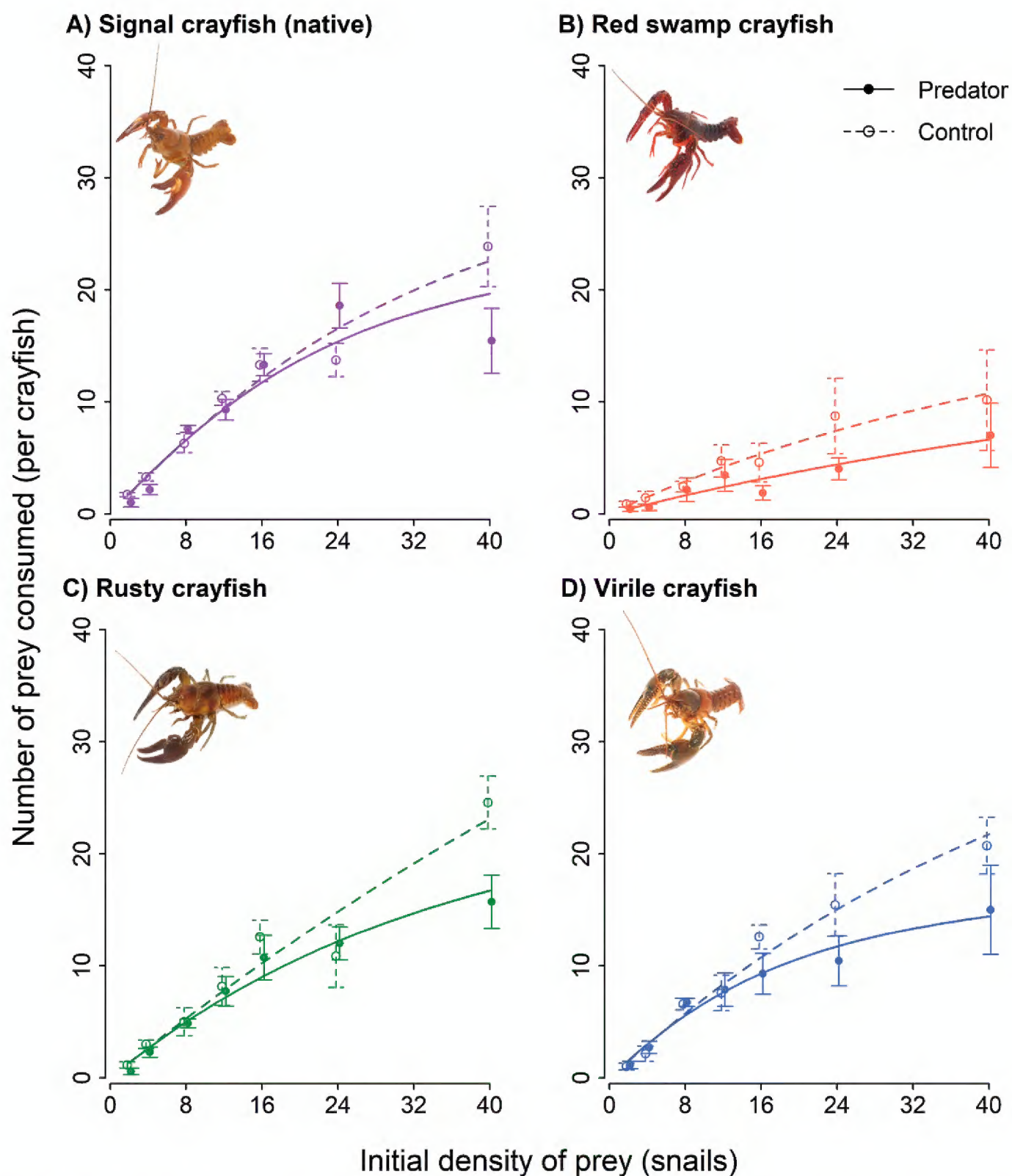
**Figure 2.** Functional responses of native and non-native crayfish feeding on snails under predator treatment and control **A** native signal crayfish **B** non-native red swamp crayfish **C** non-native rusty crayfish and **D** non-native virile crayfish. Lines represent model fit (solid line: predator treatment, dashed line: control). Points represent mean consumption and error bars represent ± SE per density (filled circles: predator treatment, open circles: control; n = 7 per initial density × treatment combination).

of literature suggesting that the response of signal crayfish to predation risk is highly variable and context-dependent (Stebbing et al. 2010; Gherardi et al. 2011b; Beattie and Moore 2018; Wood and Moore 2020b). For instance, Stebbing et al. (2010) observed altered behaviour as raised posture in signal crayfish exposed to the chemical cues of European eels (*Anguilla anguilla*), but not to European perch (*Perca fluviatilis*), whereas Hirvonen et al. (2007) reported crayfish reduced shelter use when exposed to eel odour.

**Table 2.** Functional response estimates of native and non-native crayfish species under predator treatment and control. The 1st order term of the logistic regression (see Methods), the functional response (FR) type, estimated parameters attack rate ($a$) and handling time ($h$), the maximum feeding rate ($1/hT$) and the functional response ratio (FRR). * = significant results.

| Treatment/ Species | 1st order term (p-value) | FR type | $a \pm$ SE (p-value) | $h \pm$ SE (p-value) | $1/hT$ | FRR |
|---|---|---|---|---|---|---|
| **Predator** | | | | | | |
| Signal crayfish (native) | -0.0617 (> 0.001)* | II | 2.26 ± 0.23 (> 0.001)* | 0.04 ± 0.004 (> 0.001)* | 28.02 | 63.5 |
| Red swamp crayfish | -0.0078 (0.29) | I[†] | 0.25 ± 0.05 (> 0.001)* | 0.04 ± 0.037 (0.271) | 24.81 | 6.1 |
| Rusty crayfish | -0.0283 (> 0.001)* | II | 1.16 ± 0.14 (> 0.001)* | 0.03 ± 0.006 (> 0.001)* | 31.37 | 36.3 |
| Virile crayfish | -0.0411 (> 0.001)* | II | 1.64 ± 0.23 (> 0.001)* | 0.05 ± 0.006 (> 0.001)* | 19.81 | 32.5 |
| **Control** | | | | | | |
| Signal crayfish (native) | -0.0358 (> 0.001)* | II | 2.08 ± 0.24 (> 0.001)* | 0.03 ± 0.004 (> 0.001)* | 37.53 | 78.2 |
| Red swamp crayfish | -0.0142 (0.022)* | II | 0.50 ± 0.08 (> 0.001)* | 0.04 ± 0.015 (0.021)* | 28.59 | 14.3 |
| Rusty crayfish | -0.0101 (0.086) | II | 1.14 ± 0.13 (> 0.001)* | 0.01 ± 0.006 (0.061) | 94.99 | 108.0 |
| Virile crayfish | -0.0252 (> 0.001)* | II | 1.43 ± 0.15 (> 0.001)* | 0.02 ± 0.005 (> 0.001)* | 47.95 | 68.8 |

[†]Despite being categorised as Type I using AIC, we fitted data to the Type II model to allow comparison of parameters between treatment and control.

These studies were performed in the invaded range of signal crayfish; thus, unexpected behavioural responses were attributed to naïve juvenile individuals with a lack of evolutionary history with these predators (Hirvonen et al. 2007; Stebbing et al. 2010). However, this may not be the case in our study where signal crayfish is native and has experience with largemouth bass in the region for over a hundred years. This suggests that signal crayfish may better assess the risk posed by a familiar predator using both chemical and visual cues (Blake and Hart 1993), whereas all three non-native crayfish species responded in a more conservative manner to the presence of chemical cues alone in a novel environment (Gherardi et al. 2002; Hazlett et al. 2003). Another possible mechanism is related to the larger body sizes of signal crayfish compared to other species (both in the wild and individuals used in this experiment: Table 1). There is evidence that crayfish can assess predator size through chemical cues (Wood and Moore 2020a; Wagner and Moore 2022); thus, the size of the largemouth bass in the experiment may have been too small relative to signal crayfish to elicit an antipredator behaviour resulting in reduced foraging rates.

All crayfish species presented a Type II FR, which is deemed to destabilise resource populations. This result aligns with the known impacts of these species on biomass and abundance of benthic invertebrates, particularly snails (Twardochleb et al. 2013). Moreover, when applying an FR-based metric to evaluate impacts, our native
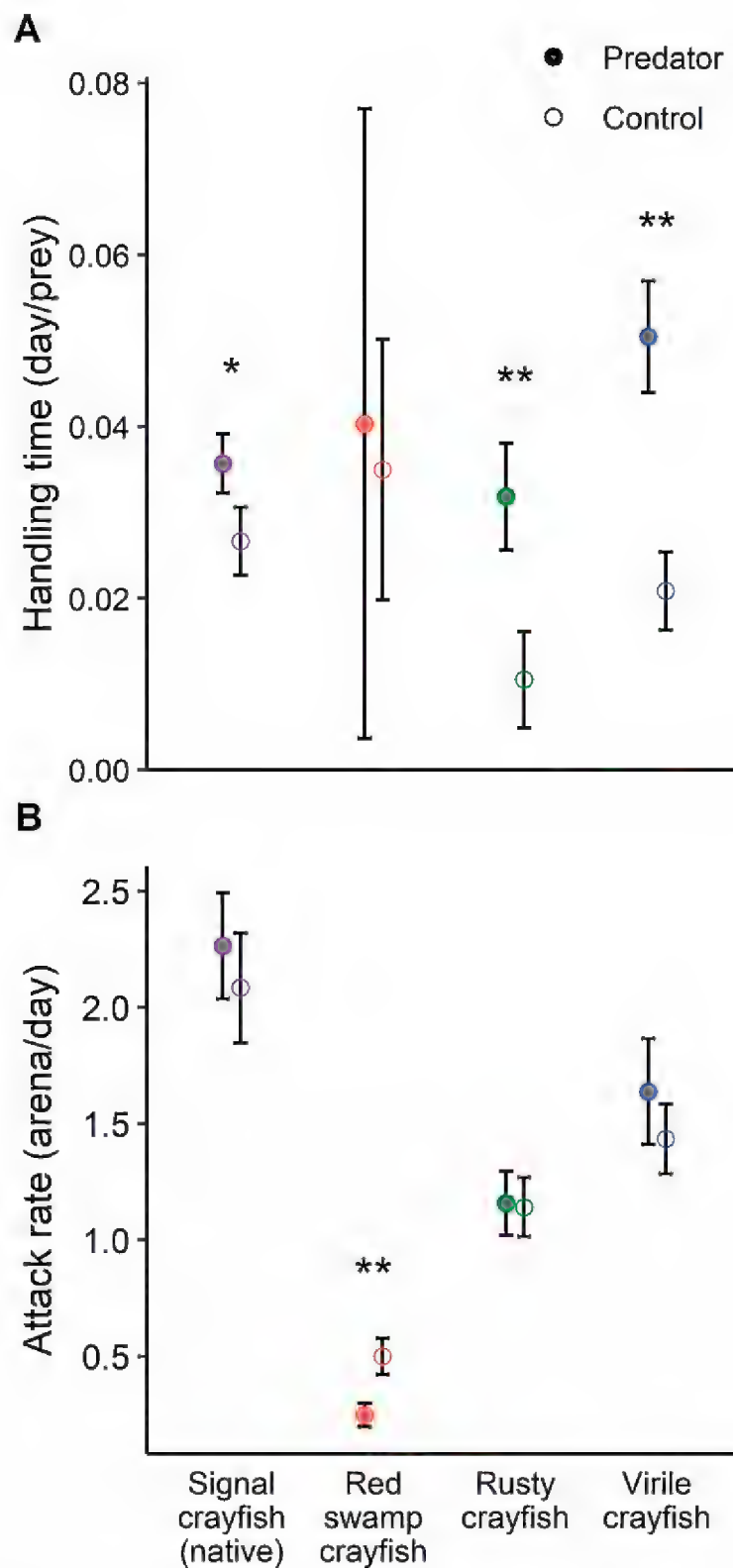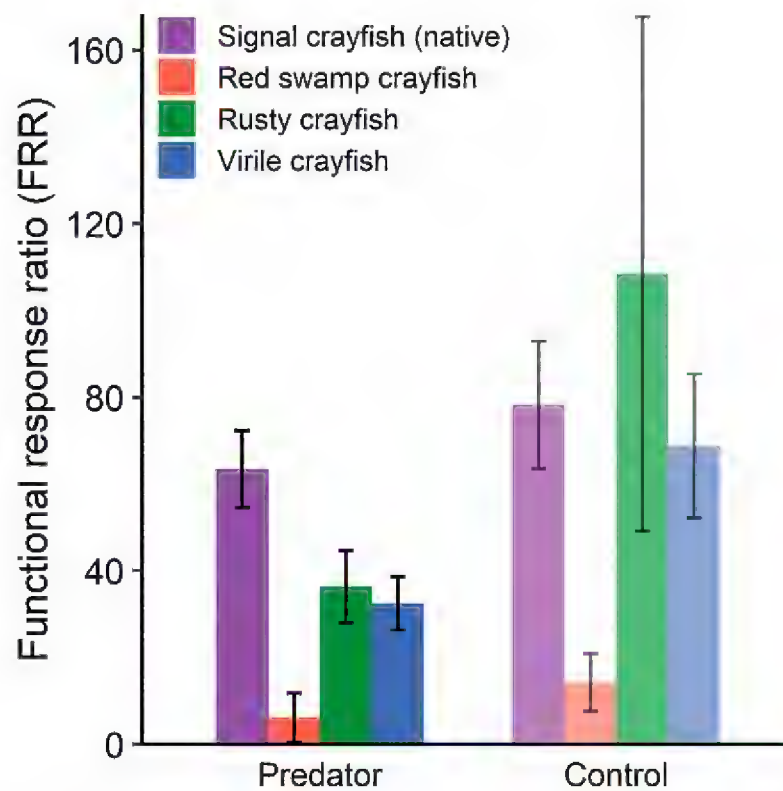
**Figure 3.** Estimated functional response parameters of native and non-native crayfish species under predator treatment and control **A** handling time parameter $h$ and **B** attack rate parameter $a$. Points represent the mean estimate of the model (filled circles: predator treatment, open circles: control) and error bars represent $\pm$ SE. $*p < 0.1$ and $**p < 0.05$.

comparator species generally showed a higher FRR than non-natives, which contradicts the pattern of invaders being more impactful than their native counterparts (Cuthbert et al. 2019). Nevertheless, signal crayfish is itself highly invasive in Europe, Japan and the south-western United States, usually reaching higher abundances than those observed in its native range (Larson and Olden 2013) and causing significant impact through their omnivorous feeding habits (Usio et al. 2009; Twardochleb et al. 2013; Vaeßen and Hollert 2015). Our results also align with a previous study that

**Figure 4.** The functional response ratio (FRR) of native and non-native crayfish species under predator treatment and control. The calculated FRR (*a/h*) is represented as bars (solid bars: predator treatment, shadowed bars: control) and error bars represent propagated standard errors of original estimates of parameters attack rate *a* and handling time *h*.

experimentally compared the predation rate of signal crayfish and non-native crayfish towards Chinese mystery snail (*Bellamya chinensis*), where native signal crayfish consumed significantly more snails of all size classes than did non-native crayfish (Olden et al. 2009). Indeed, previous studies that used the comparative FR approach to assess the impacts of signal crayfish where it is non-native found that the species generally present higher FR magnitude when compared to European native analogues, such as white-clawed crayfish (*Austropotamobius pallipes*) and noble crayfish (*Astacus astacus*), although impact varied with prey type (Haddaway et al. 2012; Rosewarne et al. 2016; Taylor and Dunn 2018; Chucholl and Chucholl 2021). Differences in experimental systems, such as diverse prey types and arena sizes, preclude us from comparing the native signal crayfish findings here to those of invasive populations of the species. Future comparative studies of the FRs of native and non-native populations are recommended.

We found significant differences amongst NNS predatory impacts towards prey. Rusty crayfish and virile crayfish showed consumption rates similar to those of native signal crayfish, whereas red swamp crayfish demonstrated the lowest feeding rate, despite the latter species being considered one of the most impactful invasive crayfish in the world (Lodge et al. 2012; Twardochleb et al. 2013). Even though all crayfish are considered omnivorous or polytrophic, there are marked differences in their predominant trophic ecology (Reynolds et al. 2013). For instance, red swamp crayfish has a lower trophic position than signal crayfish, which is consistent with the perceived impact on macrophyte communities of the former species (Matsuzaki et al. 2009; Larson et al. 2017). Similarly, Madzivanzira et al. (2021) also reported a lower FR magnitude of red swamp crayfish preying on catfish fry compared to a native analogue crab. Despite this, it

has been demonstrated that invasive populations of red swamp crayfish in Europe present ontogenetic niche shifts and have opportunistic feeding habits, adjusting its diet to different biotic and abiotic contexts, which further explains its success as an invader (Correia 2002, 2003; Carreira et al. 2017; Jackson et al. 2017). Additionally, red swamp crayfish has weaker chelae closing force compared to other decapods, which helps explain its preference for feeding on softer resources (South et al. 2020). Our findings support previously observed impacts of rusty crayfish and virile crayfish on snail communities where they are invasive (Dorn and Wojdak 2004; McCarthy et al. 2006; Kreps et al. 2012). The greater consumption rate of invasive crayfish is likely associated with selected traits, such as boldness and foraging voracity in NNS populations, which are known to differ from their native range (Pintor and Sih 2009; Reisinger et al. 2017; Glon et al. 2018).

Previous studies that investigated TMIEs using the FR approach reported mixed outcomes. Considering simple habitats, the presence of predator cues reduced consumption rates of the amphipod *Echinogammarus marinus*, an intermediate predator, towards isopod prey (Alexander et al. 2013). By contrast, fish cues did not influence the FR's magnitude of two amphipod species (the native *Gammarus duebeni* and the invasive *Gammarus pulex*) towards three different invertebrate preys (Paterson et al. 2015). Our study reinforces the need for considering the wider biological context of ecological interactions when quantifying the impacts of NNS. Moving forward, we suggest three primary ways that future studies could further explore context-dependencies.

First, the effect of abiotic contexts, such as habitat complexity and presence of shelter, continues to be a research need. The Type II FR curves reported here align with general expectations from the broader literature (Jeschke et al. 2004); however, the lack of habitat complexity in experimental arenas may prevent the observation of more stabilising Type III responses (Alexander et al. 2012; Griffen 2021). Likewise, gravel substrate has been reported to reduce crayfish consumption of pelagic, but not benthic prey (Vollmer and Gall 2014; South et al. 2019). Additionally, shelter use is a common behavioural response of crayfish to predator cues (Blake and Hart 1993; Garvey et al. 1994) and could have further magnified the observed differences between the predator treatment and control reported in our study.

Second, it would be valuable to evaluate additional biotic contexts, such as alternative resource availability, the presence of intra- and inter-specific competitors and effects of visual predator cues. For instance, prey preference for different resources, such as macrophyte or detritus, could have a significant effect on FRs for omnivorous crayfish (Cuthbert et al. 2018; Médoc et al. 2018), ultimately defining their ecological impacts when invasive (South et al. 2019; Chucholl and Chucholl 2021). Better incorporating the effects of competitive interactions in FR experiments are also fundamental to more realistic scaling of NNS *per capita* effects in the wild (Dickey et al. 2020; Latombe et al. 2022). As crayfish can respond to predation risk using a variety of different cues, the relative importance of visual and alarm cues can also be investigated using FRs (Blake and Hart 1993; Ramberg-Pihl and Yurewicz 2020). Third, future research investigations discussed above would benefit from the linking of mesocosms experiments with in-situ field studies to ensure robust scaling of our understanding (Iacarella et al. 2018).

## Conclusions

Ecological impacts of NNS are notoriously challenging to anticipate given a myriad of biotic and abiotic context-dependencies that can affect the organismal performance in nature. The comparative FR approach has been used to incorporate these context-dependencies to predict the impact of NNS, through relative comparisons of *per capita* effects (Dick et al. 2014; Cuthbert et al. 2019; Faria et al. 2023). Here we showed that the presence of a higher-order predator can alter important parameters of FR, with direct effects on maximum consumption rates and predicted impact of intermediate non-native consumers. These findings suggest that the broader biological context in which consumer activities take place should not be overlooked if we aim to understand the ecological impacts of NNS. Likewise, biogeographic origin alone is not the sole indicator of impact, as we found that native signal crayfish demonstrated the highest estimated impact on prey in the presence of predation risk by a fish predator.

The ecology of fear predicts that the cost of anti-predator behaviour is associated with reduced offspring, thus modulating consumer abundance (Zanette and Clinchy 2019). Given the immense challenges in eradicating and controlling invasive crayfish populations (Gherardi et al. 2011a; Manfrin et al. 2019), this raises the interesting question of whether chemical cues could be used as an additional management tool to reduce their short-term ecological impacts, while other control strategies are being implemented. We encourage more research on which and how chemical components of predator and dietary cues trigger behavioural responses in crayfish, as these are not entirely elucidated (Mitchell et al. 2017), but have potential management applications.

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## Supplementary material 1

### Data from functional response trials

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Data type: xls

Explanation note: Data from functional response trials for each crayfish species under predator treatment and control.

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